XIII.

The Uses and Origin of the Arrangements of Leaves in Plants.

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In proposing to treat in this paper of the *origin* of some of the more common arrangements of leaves and leaf-like organs in the higher orders of plants, I do not intend to make this question the principal object of discussion, but propose only to consider it so far as it affords useful hypotheses for the interpretation of some of the obscurer features in the main object of this inquiry; namely, questions of the *uses* of these arrangements, or of their adaptations to the outward economy of the plant's life, and to the conditions of its existence. If by such a discussion hypothesis can be made to throw light on physiological questions, while seeking more directly to connect in a continuous series the simpler and more general with the more specific and complicated forms in vegetable life, it will gain for itself a much greater interest and value than it would otherwise possess. It is, indeed, in this value of the principle of Natural Selection, its value and use as a working hypothesis, that its principal claim to respect consists. If any subsidiary hypothesis under the theory serve only as a principle of connection, a thread on which we may arrange and more clearly regard relationships that are the objects of a more promising scientific inquiry, it will at least serve a useful purpose, and even, perhaps, give greater plausibility to the theory in general of the origin of organic forms through the agency of their utilities, or through the advantages these have given to surviving forms of life.

There is hardly any animal or plant, especially of the higher orders, that has not in many of the characteristics of its structure very conspicuous adaptations to the outward conditions of its life,—to "the part it has to play in the world," or at least to the many values or advantages it has to secure. This fact has led many naturalists, whose opinion, until lately, and for a long time, has prevailed, to regard a living structure as principally, if not entirely, made up of subordinate parts or organs which exist for specific purposes, or are essentially

concerned with special services to the general life of the organism, or even to life external to it, the general life of the world, or ultimately even to the highest and best life of the world. This doctrine deprived of its grander features, as the doctrine of Final Causes in natural history, and limited simply to the conception of the parts and characters of organic structures as all, or nearly all, related essentially to the preservation and continuance of the life itself which they embody, or to the principle of self-conservation, is the ground of the importance claimed for the principle of Natural Selection in the generation of organic species. But another school of naturalists, whose influence has been steadily gaining ground, has always strenuously opposed this view, and questioned the validity of the induction on which it rests. Though it is true that the higher animals and plants exhibit a great many special adaptations to the conditions of their existence, yet, it is objected, in a far greater number of characteristics they, in common with the rest of the organic world, exhibit no such adaptations. In those most important features of organic structures, which are now called genetic characters, and were formerly called affinities, few or no specific uses can in general be discovered; and it is considered unphilosophical to base an induction on the comparatively few cases of this class of characters which have obvious utilities. It is thought unphilosophical to presume on such meagre grounds that all these characters are either now, or have been, of service to the life of the organism; thus confounding these genetic characters with those that are properly called adaptive. By positing this distinction of genetic and adaptive characters as a fundamental and absolute one, the theory of organic types opposes itself to the conception of utility as a property of organic structures in general, and conceives, on the other hand, that an organism consists essentially of certain constituent parts and characters which are of no service to its general life, and are ends, so far as we can know, in themselves; though other and subordinate ones may stand incidentally in this menial relation.

This contrast being a merely speculative difference of opinion, a reference to it, in a scientific inquiry, would be out of place were it not that scientific inquiries are almost never free from such biases. These almost always exert an unperceived influence, unless specially guarded against; and in calling attention here to this question in biological philosophy, it is only for the purpose of characterizing it as a strictly open question. As is so often the case in such debates, both sides are right and both wrong; right, so far as each refuses credence to the other's main and exclusive position, and wrong, so far as each

claims it for its own. In other words, they are not properly inductive theories, awaiting and subject to verification, but arrogant dogmas, demanding unconditional assent. The bearing of this debate on the proper questions of science relates only to *method*, or to what are the directions in which scientific pursuit and hypothesis are legitimate. It is oftener by diverting or misdirecting scientific pursuit than in any other way that such speculative opinions are of serious importance; and in this way they are purely mischievous. The theory of types is undoubtedly right in refusing assent to the doctrine, as an established induction, that every part, arrangement, or function of an organism is of some special, though it may be unrecognized, service to its life; but it is wrong in assuming, on the other hand, that all attempts at discovering uses which are not present or obvious must be futile; or, in assuming that there are characteristic features in all organisms, which are not only at present of no use, but never could have been grounds of advantage. Again, the theory of the essential reference of every feature of an organism to the conditions of its existence is undoubted right in refusing assent to this assumption of essentially useless forms, and in affirming the legitimacy of inquiries concerning the utility of any feature whatever to the life of an organism, however far removed in appearance from any relations to its present conditions of existence. It is wrong, on the other hand, in confounding the legitimacy of this pursuit with the dogma in which, as a theory, it essentially consists, or in assuming as an established induction what is only a legitimate question or line of inquiry. It is obvious, however, that a proper scientific judgment of these theories cannot be absolutely impartial, since one of them is opposed to scientific pursuit, and the other invites it. The theory of types, assuming that utility is only a superficial or incidental character, and not a property of organic forms and functions generally, occupies a negative and forbidding attitude towards what are really legitimate questions of science; and, from this point of view, judgment must be made in favor of the rival dogma. We ought to be on our guard, moreover, against this theory, since there is a strong natural, but erroneous and mischievous, tendency in the mind to fall back upon it from the difficulties of a baffled pursuit; and to regard as really ultimate those facts of which the causes and dependences elude our researches. This resort can never be justified so long as there remain any suggestions of explanation not altogether frivolous, or incapable of some degree of verification. We may safely maintain that this tendency to rest from the difficulties of scientific pursuit is the chief

cause of the prevalence at the present time of the doctrine, which, when first propounded, was regarded as heterodox and dangerous, especially as it then seemed opposed to the doctrine of Final Causes. This apparent opposition has since, however, been made to disappear by a modification of the latter doctrine, which has incorporated in it this theory of types, by representing a type of structure as an ultimate feature in the general plan of creation, or as an end for which the successive manifestations and the adaptations of life exist, or to which they tend. According to this doctrine, it is not for the sake of the maintenance and continuance of the mere life, such as it is, or such as it can be, under the conditions of its existence, that adaptations exist in organisms; but it is for the sake of realizing in it certain predetermined special types of structure, which are ends in themselves, and to which the adaptive characters of the structure are subservient. Thus an elaborate and formidable philosophical theory has grown up, which stands in direct and forbidding opposition to such inquiries as the one proposed in this discussion. If the theory were true, it would, indeed, be idle to ask what are the uses, and how could these have determined the origin of those special leaf arrangements in the higher plants, which have been observed by botanists, and discussed by mathematicians in the theory of Phyllotaxy. There is a sufficiently obvious utility in the general character of these arrangements with reference to the general external economy of vegetable life and the functions of leaf-like bodies; but this does not at first sight appear to regard the particular details, or the special laws of arrangement, with which the theory of Phyllotaxy is concerned. In these we have apparently reached ultimate features of structure, the origin or value of which in the plant's life it would, on the theory of types, be idle to seek. These are such excellent examples of what the theory of types supposes to be finalities in biological science, that botanists and mathematicians, with hardly an exception, have consented to regard them in this light. There is a difference of opinion, it is true, as to whether the several angular intervals between successive leaves around the stem, or the several angles of divergence between successive leaves in the spiral arrangements, ought to be regarded as modifications of a single typical angle to which they approximate in value, or as several distinct types. There is no difference of opinion, however, in regard to another distinction of types in leaf arrangements, which, to all appearance, are separated by entirely distinct characters; namely, the so-called spiral arrangements and those of the verticil or whorl. It is with the former chiefly that the mathematical theory

of Phyllotaxy is concerned. The latter, or the verticil arrangements, though presenting a great variety of forms, are so obviously all of the same general and simple type, that they present no difficulties or problems for the exercise of mathematical skill. Their varieties consist simply in the number of leaves in the whorl. From two leaves placed oppositely, these whorls vary through all numbers to very large ones, and in all these varieties the simple law holds that the leaves of successive whorls, being of the same number and placed in each whorl at equal distances around the stem, like the spokes of a wheel, are so disposed that the leaves of the upper whorl stand directly over the angular spaces between those of the lower one. These features of arrangement are so obviously the same adaptations as those we shall find in the more complicated spiral arrangements, that I will consider them both together. They appear to be two solutions of the same problem in the economy of the higher vegetable life; though it is probable that the whorl arrangement is the inferior one. It approaches in simplicity most nearly to the alternate system among the spiral forms, though it is perfectly distinct from this. An opposition of leaves in the whorl is an accident or trivial circumstance dependent on the fact that the number of leaves in the whorl is in many cases an even one; while in the alternate arrangement this opposition is an essential character. This would not be strictly the case, indeed, if the theory were true that the alternate as well as the other spiral arrangements are only modifications of a single typical one. But an examination of the evidence will show very slight grounds for this opinion. No doubt, in the doctrine of development, all these arrangements must be considered as modifications of some single ancient form, though this, it is quite likely, was very different from the typical arrangement, or the perfect form, in the theory of Phyllotaxy. The important point, however, to be considered here, is, that on the theory of development there is properly no genetic connection between the opposition of leaves in whorls and those of the alternate arrangement. And, indeed, in the three-leaved systems of the two types the contrast is very marked; for the three leaves of such a whorl stand over the angular spaces between the three of the whorl below it, as in other arrangements of this type; while the three leaves of the spiral system or cycle stand severally directly over the three below them. The genetic relationships of the two great types will be specially considered when we come to the problem of the origin of both from simpler vegetable forms.

The names "system" and "cycle" are not so properly applicable to groups

of leaves in the spiral arrangements as to those of whorls, and refer rather to abstract numbers, counted from any point we please, than to actually definite groups. The actual system, cycle, or group in these arrangements is of indefinite extent, or comprises the whole stem, so far as it is developed, and even extends into the undeveloped leaves of the terminal bud. In speaking of a cycle of leaves in these arrangements no definitely situated group is meant, but only a definite number counted from any one we may choose for an origin. In almost all arrangements of this type we find that, after thus counting some definite number of leaves from some one assumed as the first, we arrive next at a leaf which stands directly over the first. Such a group, so determined, makes what is called a cycle; or, as we may sometimes prefer to call it, a system. Within it leaves succeed each other at successively greater and greater heights, and are so placed around the stem that the same angular interval or angle of divergence is contained between any two successive ones. This angle of divergence is commensurate with the circumference, but is not always an aliquot part of it, as in the angular interval of the leaves of whorls. It is in many plants some multiple of an aliquot part, and in counting the leaves successively through the cycle, we have to turn several times around the stem. This number of revolutions, divided by the number of leaves in the cycle, is the ratio of the angle of divergence to the whole circumference; and the fraction expressing this ratio is used to denote the particular arrangement of such a system. Thus the fraction $\frac{1}{2}$ denotes the alternate arrangement, in which there are two leaves in one turn, the third leaf falling over the first. $\frac{1}{3}$ is the name of the three-leaved system, in which there are three leaves in one turn, the fourth falling over the first. $\frac{2}{5}$ is the name of the system in which five leaves occur in two turns, and the sixth falls over the first. In order that such definite numerical systems, or cycles, should exist in the leaves of any plant, it is only necessary that the ratio of the angle of divergence to the circumference should be some proper fraction, and this fraction would be in the same way the name of the system. But any proper fraction whatever would have the property I have pointed out; namely, that after the number of leaves denoted by its denominator, and the number of turns denoted by its numerator, the next succeeding leaf would fall over the first. Whatever may be the purpose or advantage of the spiral arrangement, and of this feature in it, it is obvious that some other purpose is sought, or some other advantage gained, by the actual arrangements of this sort in nature; or else it would appear on the

theory of types, that the typical properties of them are not fully determined by what we have yet observed respecting them. For, although there is a great variety of such arrangements, these do not include all the possible ones, nor even all the simplest. There must still be another principle of choice besides what determines the rational fraction and the spiral arrangement. What this is, is the problem of the mathematical theory of Phyllotaxy. The result of this investigation was a classification of all the fractions that occur in natural arrangements under the general form of the continued fraction

$$\cfrac{1}{a+\cfrac{1}{1+\cfrac{1}{1+\text{\&c.},}}}$$

in which a may have the values 1, 2, 3, or 4. The successive approximations of these four continued fractions give four series of proper fractions, which include all the arrangements that occur in nature. These series are for

$a=1$	$\frac{1}{2}$, $\frac{2}{3}$, $\frac{3}{5}$, $\frac{5}{8}$, $\frac{8}{13}$, &c.
$a=2$	$\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, &c.
$a=3$	$\frac{1}{3}$, $\frac{1}{4}$, $\frac{2}{7}$, $\frac{3}{11}$, $\frac{5}{18}$, &c.
$a=4$	$\frac{1}{4}$, $\frac{1}{5}$, $\frac{2}{9}$, $\frac{3}{14}$, $\frac{5}{23}$, &c.

The first series is not usually given, since they are the complements of the fractions of the second series, and express the same arrangements, but in an opposite direction around the circumference; or by supposing that the spiral line connecting the leaves is drawn from leaf to leaf the longer way round. Omitting then the first series, we shall still have in the others, as they stand, developed to five terms, many more fractions than have actually been observed, or could be observed in actual plants.

I propose in what follows to subject the mathematical induction expressed by these series to careful critical examination, to distinguish what is matter of actual observation from what is deduced from theory, and to ascertain with precision the amount of inductive evidence on which the theory of the typical angle rests. Pursuing the subject afterwards by a strictly inductive investigation, I shall estimate what there is of truth in the theory. This will lead, I think, to the rejection of the theory as it stands, or under the form of the typical angle, but will not render the observation on which it depends wholly nugatory. On the contrary, it will show that this observation really leads to the true explanation of the occurrence of only certain fractions in the spiral

arrangements, and the more frequent occurrence of some of them than of others. It is a well-known property of the fractions of these series, that after the first two in each, the others can be deduced from the preceding ones, and continued indefinitely, by a very simple process. The numerator of each after the first two is equal to the sum of the numerators of the two preceding, and its denominator to the sum of their denominators. This law, as a matter of observation, was actually discovered only in the first four fractions of the first or second series, which are by far the commonest of actually observed arrangements in nature. Other less frequently occurring fractions were arranged on the same principle, and extended so as to give the last two series. The four series, or the three lower ones, contain, therefore, more than all the fractions that are known to belong to natural arrangements. This will be sufficiently evident when we observe that the fractions $\frac{5}{8}$ and $\frac{8}{13}$ in the first series, or their complements, $\frac{3}{8}$ and $\frac{5}{13}$, in the second series, would be indistinguishable in actual measurement; since they differ from each other by $\frac{1}{104}$, or by less than a hundredth, which is much less than can be observed, or than stems are often twisted by irregular growth. For the same reason we must reject all but the first three terms of the third and fourth series as being distinguishable only in theory. We are thus left with a very slight basis of facts on which to erect the superstructure of theory. We shall see further on a still more cogent reason for calling in question the validity of this induction; namely, that limiting the evidence as we are thus obliged to do, we have still left so large a number of actually observed arrangements, that they include almost all that are possible among equally simple and distinguishable fractions within the observed limits of natural arrangements; all, in fact, but two; namely, the fractions $\frac{4}{9}$ and $\frac{3}{7}$. The range is not a narrow one, but extends from $\frac{1}{5}$ to $\frac{4}{5}$, or from $\frac{1}{5}$ to $\frac{1}{2}$, since the fractions above $\frac{1}{2}$ are complements of those below, and express the same arrangements, but in an opposite direction around the circumference. The problem of Phyllotaxy, therefore, seems at first sight to be reduced to this; not why the other fractions do occur in nature, but why these two do not? But to answer the latter question is really also to answer the former, though it will go but very little way towards justifying the theory of the typical or unique angle. It will go much further if we exclude from this list of fractions those which are of very infrequent occurrence, namely, those peculiar to the third and fourth series; or, in other words, take account of the relative frequency in nature of the several arrangements. This, indeed, entirely changes the aspects of the question, for we

find that, instead of two, there are six fractions of the simpler denominations (or within the limits of distinguishable values), which either do not occur in nature at all, or occur very rarely; while those that are common are four in number, or less than half of all. But we shall find that those of the six which occur rarely differ from the two really unique ones among them, and agree with the common ones in respect to the law on which the answer to our question really depends. This answer will be found to depend on the law which was observed in the first four fractions of the first or second series, and was extended in the continuation of these and the formation of the others. This law, or the dependence of these fractions on each other, was seen to be a simple case of the relations of dependence in the successive approximations of continued fractions, and thus lead to the induction of these fractions; namely, the continued fraction $\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{1+\&c.}}}$ for the first series, or $\cfrac{1}{2+\cfrac{1}{1+\cfrac{1}{1+\&c.}}}$ for the second. The ultimate values of these continued fractions extended infinitely are complements of each other, as their successive approximations are, and are in effect the same fraction; namely, the irrational or incommensurate interval which is supposed to be the perfect form of the spiral arrangement. This does, in fact, possess in a higher degree than any rational fraction the property common to those which have been observed in nature; though practically, or so far as observation can go, this higher degree is a mere refinement of theory. For, as we shall find, the typical irrational interval differs from that of the fraction $\frac{3}{8}$ (and its complement differs from $\frac{5}{8}$) by almost exactly $\frac{7}{1000}$, a quantity much less than can be observed in the actual angles of leaf-arrangements. The conception of such a typical angle as an actual value in nature, and as a point of departure for more specialized ones, existing either among the normal patterns, or formative principles of vegetable life, as the theory of types supposes, or in some unknown law of development or physiological necessity, — such a conception is a very attractive one. And as exhibiting in the abstract and in its most perfect form a property peculiar, as we shall see, to natural arrangements, but belonging to them in inferior and in various degrees, — as exhibiting this separated from the property which such arrangements

also have, by which they are divisible into limited systems or cycles, — from this point of view the conception acquires a valid scientific utility. But we should be on our guard against a misconstruction of it. There is no evidence whatever, and there *could* be none from observation, that any such separation of properties actually occurs in nature, or that one is superposed on the other in successive stages of development in the bud, or that this typical arrangement is first produced and subsequently modified into the more special ones, — into the limited systems or cycles represented by simple rational fractions. To suppose this is to confound abstractions with concrete existences, or would be an instance of the so-called "realism" in science, against which it is always so necessary to be on our guard. There is no reason to suppose that one rather than the other of these properties appears first in the incipient parts of the bud, or that either exists in any degree of perfection before the development of these parts has made considerable advance.

I now propose to show what this property is, which the typical or unique angle has in the abstract and in perfection, and to show what its utility is in the economy of vegetable life. And to avoid all theoretical biases I propose, as I have said, to make the inquiry a strictly inductive investigation. Taking the first of the series of fractions given above and the complements of the third and fourth, we have,

$$\begin{array}{llllll} \frac{1}{2}, & \frac{2}{3}, & \frac{3}{5}, & \frac{5}{8}, & \frac{8}{13}, & \&c. \\ \frac{2}{3}, & \frac{3}{4}, & \frac{5}{7}, & \frac{8}{11}, & \frac{13}{18}, & \&c. \\ \frac{3}{4}, & \frac{4}{5}, & \frac{7}{9}, & \frac{11}{14}, & \frac{18}{23}, & \&c. \end{array}$$

These contain all, and more than all, the distinguishable arrangements of the spiral type; but they are the intervals reckoned the longer way round. I have adopted this mode of expressing these arrangements, partly for the purpose of varying the investigation, and partly because it is better adapted to the graphical representation of these, as well as other possible arrangements, which are given in the accompanying diagram. It will be seen that the same law holds in the series here given as in those given above; yet these cannot be represented by the same general formula; but the formula becomes, $\cfrac{1}{1+\cfrac{1}{a+\cfrac{1}{1+\cfrac{1}{1+\&c.}}}}$, in which a is 1, 2, or 3. For the first of these series, or for the intervals most

frequent in nature, $a = 1$, and if we denote by k the ultimate value to which the fractions of this series more and more approximate, or what is supposed to be the type form of them, then, since $k = \cfrac{1}{1 + \cfrac{1}{1 + id.\ ad\ inf.}}$, we have $k = \frac{1}{1+k}$. Hence $k + k^2 = 1$, or $k^2 = 1 - k$. In the form of a proportion this is, $1 : k = k : 1 - k$; or k is the ratio of the extreme and mean proportion. Its value found by solving this equation is $k = \frac{1}{2}(\sqrt{5} - 1) = 0.6180$, approximately. From the above equation we obtain by multiplying by k successively the following: $k^2 = 1 - k$; $k^3 = k - k^2$; $k^4 = k^2 - k^3$, and in general $k^n = k^{n-2} - k^{n-1}$; that is, any power of this quantity is equal to the difference between the two next lower powers. Its square is equal to its complement; the cube to the difference between it and its square or complement, and so on. Or $k = 0.618$; $k^2 = 0.382$; $k^3 = 0.236$; $k^4 = 0.146$; $k^5 = 0.090$, etc. On this peculiar arithmetical property of k depends the geometrical one of the spiral arrangement, which it represents; namely, that such an arrangement would effect the most thorough and rapid distribution of the leaves around the stem, each new or higher leaf falling over the angular space between the two older ones which are nearest in direction so as to subdivide it in the same ratio, k, in which the first two, or any two successive ones, divide the circumference. But according to such an arrangement there could be no limited systems or cycles, or no leaf would ever fall exactly over any other; and, as I have said, we have no evidence, and could have none, that this arrangement actually exists in nature. To realize simply and purely the property of the most thorough distribution, the most complete exposure of the leaves to light and air around the stem, and the most ample elbow-room or space for expansion in the bud, is to realize a property that exists separately only in abstraction, like a line without breadth. Nevertheless practically, and so far as observation can go, we find that the last two fractions, $\frac{5}{8}$ and $\frac{8}{13}$, and all further ones of the first series, like $\frac{13}{21}$, etc., which are all indistinguishable as measured values in the plant, do actually realize this property with all needful accuracy. Thus $\frac{5}{8} = 0.625$; $\frac{8}{13} = 0.615$; and $\frac{13}{21} = 0.619$; and differ from k by 0.007, 0.003, and 0.001, respectively; or they all differ by inappreciable values from the quantity which might therefore be made to stand for all of them. But in putting k for all the values of the first series after the first three, it should be with the understanding that it is not so employed in its capacity as the grand type, or the source of the distributive character which they have;

in its capacity as an irrational fraction, — but simply as being indistinguishable practically from these rational ones, and as being entirely consistent practically with the property that rational proper fractions also have of forming limited systems or cycles. Much mystification has come from the irrational character of this fraction; scepticism on the part of non-mathematical botanists, and mysticism on the part of mathematicians. The simpler or the first three fractions of this series have also in a less degree the same distributive quality, and so in a still less degree have the fractions of the two lower series. But all the fractions left among possible ones, within the limits considered, that are sufficiently simple to be readily identified, are the fractions $\frac{4}{7}$ and $\frac{5}{9}$, or their complements $\frac{3}{7}$ and $\frac{4}{9}$; and these exceptions, as I have said, are all the grounds of fact which at first sight give any plausibility to the theory of Phyllotaxy, or make its laws anything other apparently than the necessary consequences of purely numerical properties in the simpler fractions. Yet beside the fact that these two have not the distributive character of the others, the fact should be taken account of, that by confining ourselves to the limits $\frac{1}{2}$ to $\frac{4}{5}$ we have neglected several other simple fractions, that are even worse adapted for the purpose which the great majority appear to serve. These fractions are $\frac{5}{6}$, $\frac{6}{7}$, $\frac{7}{8}$, and $\frac{8}{9}$, or their complements. Moreover, we should consider that as the fractions peculiar to the two lower series are much less fitted for this purpose than those of the first series, so they are much less frequently found in nature. Taking account of all these facts, we find the hypothesis that nature has chosen certain intervals in the spiral arrangements of leaves, and for the purpose I have indicated, to be sufficiently probable to justify a more careful consideration of it. Wide divergences from the most perfect realization of this purpose, such as we have among the more frequent forms in the fractions $\frac{1}{2}$ and $\frac{2}{3}$, or in the alternate and three-leaved systems, and also among the less frequent forms, indicate the existence of other conditions or purposes in these arrangements, which I propose to consider further on. I may remark here, however, that these two classes of exceptions from the most perfect realization of the distributive property, namely, those of the first series which belong to the most advanced forms of life, and those peculiar to the two other series, are probably due to widely different causes; the one having, in fact, a high degree of specialization, and the other falling short in respect to this distributive property on account of a low degree of specialization. This view, which is one of the consequences of theoretical considerations on the *origin* of these arrangements, that will be presented when we come to consider the

origin of spiral arrangements in general, and of the whorl, is significantly in accordance with the observation that the forms peculiar to the two lower series are more frequent among fossil plants than among surviving ones.

But waiving these theoretical considerations for the present, I will now examine, quite independently of theory, the properties in the spiral arrangements of all the fractions between $\frac{1}{5}$ and $\frac{4}{5}$, or rather between $\frac{1}{2}$ and $\frac{4}{5}$, and of a less denomination than 14ths. I adopt these limits because the character of all fractions greater than $\frac{4}{5}$, or less than $\frac{1}{5}$, will be sufficiently shown by this limit, and because fractions less simple than 13ths cannot be distinguished in nature from simpler ones. The fractions between $\frac{1}{2}$ and $\frac{1}{5}$, being complements of those greater than $\frac{1}{2}$, need not, of course, be separately studied; since they express the same arrangements, only counted in the opposite direction around the stem. I have chosen to represent these possible arrangements by the larger fractions rather than by the smaller (their complements), for reasons I have given, although theoretical considerations on the origin of spiral arrangements in general suggest the latter and more usual mode as the proper one. This may be given as an additional reason for the choice, since we shall not thus be led to confound a conventional mode of representation with a law of nature, or have any undue bias in consequence, but shall be able to judge the hypothesis on its own merits. The best reason, however, for the choice is, that by representing the cycle by the larger number of turns, or by counting the longer way round, we are able to spread out into greater detail in the accompanying diagram the steps of the distribution, and see more clearly its character.

In the following table the first column contains all the fractions I have defined, arranged in the order of their denominations, with their decimal equivalents to thousandths, and at the end the irrational quantity k, with its approximate decimal value. The second column contains the same fractions, arranged in the order of their magnitudes, with their decimal values and the differences between successive ones. The third contains the complements of these decimal values. They represent the smaller of the two parts or angles of divergence into which two successive leaves would divide the circumference, or represent these angles reckoned the shorter way round. The fourth contains the differences between the decimals of the second and third, together with the ratios of these to those of the third. (These differences are occasionally corrected by a unit, to allow for the inexactness or the approximate character of some of these decimals.) They are the subintervals or angles of divergence introduced by the third leaf of a cycle between it and the first:

$\frac{1}{2}$	.500	$\frac{1}{2}$	.500	38	.500	.000	∞
$\frac{2}{3}$	.667	$\frac{7}{13}$	.538	7	.462	.076	6
$\frac{3}{4}$	.750	$\frac{6}{11}$	.545	11	.455	.091	5
$\frac{3}{5}$	.600	$\frac{5}{9}$	.556	15	.444	.111	4
$\frac{4}{5}$	.800	$\frac{4}{7}$	.571	12	.429	.143	3
$\frac{4}{7}$	.571	$\frac{7}{12}$	.583	17	.417	.167	$2\frac{1}{2}$
$\frac{5}{7}$	.714	$\frac{3}{5}$	.600	15	.400	.200	2
$\frac{5}{8}$	.625	$\frac{8}{13}$	.615	3	.385	.231	$1\frac{2}{3}$
$\frac{5}{9}$	.556	k	.618	7	.382	.236	$\frac{1}{k}$
$\frac{7}{9}$	.778	$\frac{5}{8}$	.625	11	.375	.250	$1\frac{1}{2}$
$\frac{7}{10}$	.700	$\frac{7}{11}$	.636	31	.364	.272	$1\frac{1}{3}$
$\frac{6}{11}$	.545	$\frac{2}{3}$	.667	25	.333	.333	1
$\frac{7}{11}$	.636	$\frac{9}{13}$	.692	8	.308	.384	$\frac{4}{5}$
$\frac{8}{11}$	.727	$\frac{7}{10}$	.700	14	.300	.400	$\frac{3}{4}$
$\frac{7}{12}$	.583	$\frac{5}{7}$	.714	13	.286	.428	$\frac{2}{3}$
$\frac{7}{13}$	.538	$\frac{8}{11}$	.727	23	.273	.454	$\frac{3}{5}$
$\frac{8}{13}$	.615	$\frac{3}{4}$	.750	19	.250	.500	$\frac{1}{2}$
$\frac{9}{13}$	.692	$\frac{10}{13}$	.769	9	.231	.538	$\frac{3}{7}$
$\frac{10}{13}$	.769	$\frac{7}{9}$	.778	22	.222	.556	$\frac{2}{5}$
k	.618	$\frac{4}{5}$	.800		.200	.600	$\frac{1}{3}$

The first point to be noticed in this table is the character of the ratios in the last column. For all the fractions here given of less magnitude than $\frac{3}{5}$, (or whose complements are greater than $\frac{2}{5}$,) the first subinterval is contained in the preceding, or in the smaller of the primary intervals, several times, or more than twice. To the interval $\frac{1}{2}$ or in the alternate arrangement there is no secondary interval. The cycle is completed at once, and no distribution is effected, except the simple opposition of successive leaves. The next following fractions $\frac{7}{13}$ and $\frac{6}{11}$ have a similar character in respect to the property of distribution; that is, the subinterval introduced by the third leaf would, in these, be very small, being respectively 6 and 5 times smaller than the smaller primary interval. But they have not the cyclic simplicity of the alternate system, and thus lack whatever advantage belongs to it. The same is true in diminishing degrees of the following fractions, until we arrive at $\frac{3}{5}$; and none of these occur in nature. $\frac{3}{5}$ is the first in order of magnitude after $\frac{1}{2}$ which is found in nature, and immediately following it, we find all the other phyllotactic fractions of the first series, or all the fractions that are of common occurrence in nature, except $\frac{1}{2}$. The bracket includes these, and also one intruder, namely, $\frac{7}{11}$. The ratios in the last column range for these fractions from 2 to 1; indicating that for all these the subinterval introduced by the third leaf, though less than the smaller primary interval, is not contained in it more than twice. For the last fraction of this series, $\frac{2}{3}$,

this subinterval is equal to the smaller primary one; the third leaf falls exactly in the middle of the larger interval and completes the cycle. This fraction is thus next in cyclic simplicity to $\frac{1}{2}$, and has but little more of the distributive character. Following $\frac{2}{3}$ we find two fractions, $\frac{9}{13}$ and $\frac{7}{10}$, which resemble it in this respect as $\frac{7}{13}$ and $\frac{6}{11}$ resemble $\frac{1}{2}$, and lacking like them the cyclic simplicity of their type they have still no superiority to it in the distributive property. The same is true in diminishing degrees of the following fractions. But these onward to the end are, with one intrusive exception, phyllotactic fractions of the two lower series, or those of infrequent occurrence in nature. They include all the fractions peculiar to these series, that is, all but $\frac{2}{3}$, just as the group above includes all of the first series except $\frac{1}{2}$; and these two fractions have the least of the distributive character and most of cyclic simplicity. They are the fractions of the smallest denominations, and might properly be separated from the others as a special type; with more propriety, indeed, than the purely distributive fraction k could be separated from others of the first group. In all the fractions of the lower group the disparity of the primary intervals, or the great difference between these fractions and their complements (the differences exceeding these complements, and the ratios being proper fractions), unfit them for a distributive arrangement, so far at least as the earlier steps of the cycle or the first three leaves are concerned. In other words, the primary intervals being in greater ratios than two to one, the distribution is imperfect at the outset. But it is better in subsequent leaves, for all those fractions that are found in nature, or for all but the one intrusive exception I have referred to. This exception is the fraction $\frac{10}{13}$, which, as well as $\frac{7}{11}$ in the first group, seems at first sight a remarkable anomaly. They are not, as we shall see, anomalies at all; but, though differing from the other fractions of these groups in the character of the distribution higher up in the cycles than the steps we have yet considered, namely, the first three leaves, yet they occur thus isolated in these groups only on account of the arbitrary limit I have assumed for the denominations of the fractions in the table, or the limit of 13ths. If fractions of higher denominations had been included in the table, other exceptional fractions would have appeared within the limits of these groups. But before proceeding to show this, I will call attention to one other fact shown by this table, namely, how large within the limits assumed for the table the number of phyllotactic fractions is, compared to the whole number, namely, more than half. Out of the nineteen possible proper fractions given in the table, ten are phyllotactic; that is, either actually

occur in nature, or are deduced from theory. The theoretical source of many of them, of more than half, is more than probable; for the limit of the denominations assumed for the table is undoubtedly beyond the limits of distinguishable forms in actual measurements. If, however, this assumed limit had been less, the number of the other fractions would have been reduced in greater proportion than the phyllotactic ones. If it had been greater, they would have been increased in a greater proportion. In other words, the ratio of the number of fractions given by the theory of Phyllotaxy to all other possible ones within the same range of denominations decreases from a very large value (nearly the whole) to smaller and smaller values. This ratio, therefore, is a fact of no importance as a fact of observation, since it is almost wholly a formal fact, not a material one, as the logicians say; or is involved in the form of expression, or of representation, or in the nature of the method of investigation. The important fact is that there are fractions, however few, which would be distinguishable if they existed in nature, but are not found, though their magnitudes are within the range of those that do exist. Such are the fractions $\frac{4}{7}$ and $\frac{5}{9}$. If the fractions of our table were arranged, not only in the order of their magnitudes, but at corresponding distances, and if we disregarded altogether the character of simplicity or complexity in these fractions, and the numbers of them within any limit of denomination, and considered only the ranges of geometrical values between them, we should find between $\frac{1}{2}$ and $\frac{3}{5}$ a difference of $\frac{1}{10} = 0.100$ of the circumference, which is greater than the whole range of the other fractions of Phyllotaxy in the first group, namely, $\frac{1}{15} = \frac{2}{3} - \frac{3}{5} = 0.067$ of the circumference; and between the last of these and the first fraction of the second group we have the difference $\frac{5}{7} - \frac{2}{3} = \frac{1}{21} = 0.047$ of the circumference, which is not much less than the range $\frac{1}{15}$. In these two spaces, therefore, of $\frac{1}{10}$ and $\frac{1}{21}$, there would be room for fractional intervals as distinguishable from each other as those of the first group are; though, in the space $\frac{1}{21}$, or 0.047, between the first and second groups, no simple fractions, or of less denomination than $\frac{7}{10}$, could occur, and no interval has been observed which belongs to either of these spaces. It is therefore sufficiently obvious that the fractions $\frac{5}{9}$ and $\frac{4}{7}$ (which would, perhaps, be with difficulty distinguished from each other, since they differ by only $\frac{1}{63}$) are real omissions from natural arrangements. $\frac{9}{13}$ and $\frac{7}{10}$ would be really indistinguishable from each other if they existed; but the former could be as readily distinguished from any real arrangements as these are from one another. It ought, therefore, to be regarded as also a real exception,

though it may have been omitted not only on account of its defective character as a distributive fraction, but also for its lack of simplicity. Taking account of the relative frequency of the fractions that are found in nature, we have sufficient grounds to suppose that the distributive character of them is an utility of actual importance to the welfare of plants.

But I have not yet shown this distributive character throughout the cycle, or what distinguishes them from the abnormal forms I have referred to. I must first show, however, that these are only apparent anomalies, and that others of the same character would occur if the table were extended. There is a ready means of extending the table; the same law in fact which holds in the series given above. Each value of the proper fractions, as arranged in the second column, except the extreme ones, can, it will be seen, be derived from the preceding and following ones by adding their numerators for a new numerator, and their denominators for a new denominator, and, in some cases, reducing the fraction thus obtained to lower terms. Moreover, in the table as it stands, the difference of any two successive fractions is the reciprocal of the product of their denominators, or when reduced to this as a common denominator, their numerators differ by a unit. From this property it follows in the theory of numbers that intermediate values obtained in this way cannot be reduced to lower terms, and are the fractions of the smallest denomination intermediate in value between any two. It is obvious that by this process the table could be extended indefinitely, without omitting any fraction of less than any assignable denomination. Indeed, it could have been constructed from its limits by successive interpolations of this sort. Thus taking the extreme limits $\frac{1}{2}$ and 1, or, as we may express the latter, $\frac{1}{1}$, which differ by $\frac{1}{2}$, or the reciprocal of the product of their denominators, we obtain between them by this process $\frac{2}{3}$. Between $\frac{1}{2}$ and $\frac{2}{3}$ we find $\frac{3}{5}$. Between $\frac{2}{3}$ and $\frac{1}{1}$ we find $\frac{3}{4}$. Continuing this process, as in the subjoined example, we arrive at the results in the lower line, which are, many of them, of higher denomination than those of the table.

$$\frac{1}{2} \qquad \frac{2}{3} \qquad \frac{1}{1}$$

$$\frac{3}{5} \qquad \frac{3}{4}$$

$$\frac{4}{7} \qquad \frac{5}{8} \qquad \frac{5}{7} \qquad \frac{4}{5}$$

$$\frac{5}{9} \qquad \frac{7}{12} \qquad \frac{8}{13} \qquad \frac{7}{11} \qquad \frac{7}{10} \qquad \frac{8}{11} \qquad \frac{7}{9} \qquad \frac{5}{6}$$

$$\frac{1}{2}, \frac{6}{11}, \frac{5}{9}, \frac{9}{16}, \frac{4}{7}, \frac{11}{19}, \frac{7}{12}, \frac{10}{17}, \underbrace{\frac{3}{5}, \frac{11}{18}, \frac{8}{13}, \frac{13}{21}, \frac{5}{8}, \frac{12}{19}, \frac{7}{11}, \frac{9}{14}, \frac{2}{3}}, \frac{9}{13}, \frac{7}{10}, \frac{12}{17}, \underbrace{\frac{5}{7}, \frac{13}{18}, \frac{8}{11}, \frac{11}{15}, \frac{3}{4}, \frac{10}{13}, \frac{7}{9}, \frac{11}{14}, \frac{4}{5}}, \frac{9}{11}, \frac{5}{6}, \frac{6}{7}, 1.$$

By interpolating one more value between the first two of these fractions, or between $\frac{1}{2}$ and $\frac{6}{11}$, namely, $\frac{7}{13}$, and by omitting those of higher denominations, we obtain all the proper fractions of our table. Among these higher denomi-

nations we find several new intruders in the phyllotactic groups, namely, $\frac{11}{18}$, $\frac{12}{19}$, and $\frac{9}{14}$ in the first, and $\frac{11}{15}$ in the second, as well as new fractions of the series, namely, $\frac{13}{21}$ of the first, $\frac{13}{18}$ of the second, and $\frac{11}{14}$ of the third series, which our limits had excluded from the table; and several others beyond these groups. If, on the other hand, we make the denominations of our table smaller, and exclude all above 9ths, as being either actually indistinguishable, or with difficulty distinguished from the remaining ones, we have remaining $\frac{1}{2}$, $\frac{5}{9}$, $\frac{4}{7}$, $\frac{3}{5}$, $\frac{5}{8}$, $\frac{2}{3}$, $\frac{5}{7}$, $\frac{3}{4}$, $\frac{7}{9}$, $\frac{4}{5}$, all of which are included in observed arrangements, except the two, $\frac{5}{9}$ and $\frac{4}{7}$. Our problem would therefore, as I have said, appear to be why these have been excluded from natural arrangements, rather than why the others have been adopted or preserved. But the problem is more correctly as follows: Account ought to be taken of the relative frequency of them, or weights ought to be attached to them according to this consideration. The weight of these two fractions would then be nothing. The weights of several others would be very small. Now, what has determined these weights? This is our problem. The superior distributive character of the more frequently occurring ones, is the only conceivable answer. We see from this, however, that we ought not to attribute to Natural Selection the existence of the spiral arrangements in general, at least not on account of the distributive property we have considered, for, in fact, they include almost all possible intervals, as the arrangements of the whorl do, and little selection is shown in them independently of their relative frequency. This relative frequency, or infrequency, in nature, amounting to total exclusion in the case of these two fractions, is, then, the only way in which Natural Selection could have been concerned in producing or modifying the spiral arrangements, so far as that property of distribution is concerned which is exhibited most perfectly by the typical or unique angle of the theory of Phyllotaxy. But, supposing these arrangements to have come into existence through some other agency, or by Natural Selection acting on some other ground of utility, or under some other phase of this one, we then see sufficient reasons why, on this principle, they should be what they are.

We might exclude altogether from our consideration the intrusive angle in our table, $\frac{7}{11}$, as being a purely theoretical product, and indistinguishable in nature from the simpler fraction above it, $\frac{5}{8}$; but I will include it in the further discussion of this group, for the sake of showing that it would, probably, have been excluded from nature, if plants had been more accurately constructed; and would not, therefore, be found, even if we had the power to distinguish it.

This discussion will also show the resemblance of the distributive character of the other arrangements of this group, as we ascend the cycle beyond the third leaf, to the theoretical unique angle. In these, as in this angle *k*, the successive subintervals are simply the differences of the two preceding ones, continually diminishing, but growing nearer and nearer in value until they become all the same aliquot parts of the circumference; namely, that expressed by the denominator of the fraction. This will be best seen in the accompanying diagram. For the numerical illustration of it, let us take each fraction of this group, and its complement; then the difference of these; then the difference of this from the complement, and so on. We have in this way:—

$\frac{3}{5} \cdot \frac{2}{5} \cdot \frac{1}{5} \cdot \frac{1}{5} \cdot 0.$

$\frac{8}{13} \cdot \frac{5}{13} \cdot \frac{3}{13} \cdot \frac{2}{13} \cdot \frac{1}{13} \cdot \frac{1}{13} \cdot 0.$

$k.\ k^2.\ k^3.\ k^4.\ k^5.\ k^6.$ &c.

$\frac{5}{8} \cdot \frac{3}{8} \cdot \frac{2}{8} \cdot \frac{1}{8} \cdot \frac{1}{8} \cdot 0.$

$\frac{7}{11} \cdot \frac{4}{11} \cdot \frac{3}{11} \cdot \frac{1}{11} \cdot \frac{2}{11} \cdot (?)$

$\frac{2}{3} \cdot \frac{1}{3} \cdot \frac{1}{3} \cdot 0.$

It will be seen by the (?) in the series for $\frac{7}{11}$, that it violates the law which holds in all the other fractions. The fourth interval, or the second subinterval, is contained three times in the preceding one, instead of once, with a smaller remainder, or exactly twice without remainder as in the others. It completes the cycle finally like the others, but introduces into it at the end of the second and in subsequent turns great inequalities side by side. If these were of sufficient absolute amount to be of importance in nature, we might be sure that such an arrangement would never exist. But a twist of the stem by only one eighth of the circumference in the length covered by eleven leaves, or a twist of one eleventh in the range of eight leaves, would convert this arrangement into the $\frac{5}{8}$ system, or the $\frac{5}{8}$ into this. We may see from this illustration how much the mathematical theory of Phyllotaxy has refined upon the facts of observation.

The property thus exhibited by the first group belongs also to the second group, or the less frequently occurring fractions, but only after the first revolution. The complement of each of these fractions, or the smaller of the primary intervals, is contained more than twice in the larger, or in the fraction itself. We must, therefore, subtract from these fractions the largest multiple of their complements contained in them for a first difference or subinterval, and then proceed as in the above cases. This gives:—

$\frac{5}{7} \cdot \frac{2}{7} \times 2 \cdot \frac{1}{7} \cdot \frac{1}{7} \cdot 0.$

$\frac{8}{11} \cdot \frac{3}{11} \times 2 \cdot \frac{2}{11} \cdot \frac{1}{11} \cdot \frac{1}{11} \cdot 0.$

$\frac{3}{4} \cdot \frac{1}{4} \times 2 \cdot \frac{1}{4} \cdot 0.$

$\frac{10}{13} \cdot \frac{3}{13} \times 3 \cdot \frac{1}{13} \cdot \frac{2}{13} \cdot (?)$

$\frac{7}{9} \cdot \frac{2}{9} \times 3 \cdot \frac{1}{9} \cdot \frac{1}{9} \cdot 0$

$\frac{4}{5} \cdot \frac{1}{5} \times 3 \cdot \frac{1}{5} \cdot 0.$

Here, as before, the intrusive angle $(\frac{10}{13})$ is found to violate the law which holds for the other fractions beyond the first turn. The first difference or subinterval is contained three times in the second or the smaller primary interval. But here, also, as

before, this fraction differs insensibly from a simpler one near it, namely, $\frac{7}{9}$. All the other fractions of our table will be found by an inspection of the diagram to violate in the same way the law in which the observed values of natural fractions, as well as the deduced ones of theory, agree. They all introduce side by side in the more advanced phases of the cycle intervals in greater ratios than two to one.

The diagram is constructed as follows: The fractions, for convenience, are in an order the inverse of that in the table. The horizontal lines represent the developed helices or spiral paths connecting ideally the successive leaves on the stem the longer way round. These are divided by the vertical lines into lengths representing single revolutions or turns around the stem. Above each line, except for k, the smaller dots (when their places are not occupied by the larger triangular dots) represent the horizontal places or directions in which the leaves fall in the cycle, and are distant successively from each other by that part of the circumference denoted by the denominator of the fraction. Above the lines are also placed the larger dots to represent the leaves as they are introduced at the constant angle represented by the fraction. After the turn in which each is introduced, dots are placed below the line in corresponding positions for all subsequent turns; and when the cycle is completed (as happens with all but k and two rational fractions within the length of the eight turns here represented), the completed cycle is repeated on parallel lines below. We are thus enabled by mere inspection to see how each new leaf would be introduced in these several arrangements in relation to the two older ones that are nearest it in horizontal direction. Thus the fractions $\frac{7}{13}$ and $\frac{6}{11}$ resemble $\frac{1}{2}$, or the alternate system, in crowding the leaves together on opposite sides of the stem, and permitting large intermediate spaces; but they do not bring them into the perfect vertical allignment of this system. The same is true in diminishing degrees of the fractions above them, as $\frac{5}{9}$, $\frac{4}{7}$, $\frac{7}{12}$, until we come to $\frac{3}{5}$. In all these cases spaces or subintervals exist side by side in greater ratio than two to one. It can be seen among the fractions next following of the first group how little the theoretical value k differs from $\frac{8}{13}$, or even from $\frac{5}{8}$, the fourteenth leaf falling only a little (by about $\frac{1}{30}$ of a turn) beyond the position of the first, instead of falling exactly over it, as it does for $\frac{8}{13}$. All the fractions of the actual arrangements of nature, as well as the less simple theoretical ones of Phyllotaxy, have the property, that after the first turn of the cycle, and also in this first turn for all the fractions of

the first series, or for those most commonly occurring in nature, *each leaf of the cycle is so placed over the space between older leaves nearest in direction to it as always to fall near the middle, and never beyond the middle third of the space, or by more than one sixth of the space from the middle, until the cycle is completed, when the new leaf is placed exactly over an older one.* This property depends mathematically on the character of the continued fractions, of which these fractions are the approximations, according to the theory of Phyllotaxy. The denominators in the characteristic part of the continued fractions, or for the whole in the case of the fractions of the first group, are each a unit *plus* a fraction, which, at the end, is also a unit, or the last denominator is 2, or $1+\frac{1}{1}$. The first denominator is the ratio of the larger primary interval to the whole circumference. These denominators are, in fact, the ratios of the successive intervals and subintervals of our diagram. The other fractions, expressed in the form of continued ones, would have denominators expressing, in the same way, the ratios of the successive subintervals, which the diagram represents; and fractions in general may be classified according to their special forms as continued fractions. Thus we have:—

$$\frac{2}{3}=\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{1}}}\qquad \frac{3}{5}=\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{2}}}\qquad \frac{4}{7}=\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{3}}}\qquad \frac{5}{9}=\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{4}}}\qquad \frac{6}{11}=\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{5}}}\qquad \frac{7}{13}=\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{6}}}$$

Again we have:—

$$\frac{3}{4}=\cfrac{1}{1+\cfrac{1}{2+\cfrac{1}{1}}}\qquad \frac{5}{7}=\cfrac{1}{1+\cfrac{1}{2+\cfrac{1}{2}}}\qquad \frac{7}{10}=\cfrac{1}{1+\cfrac{1}{2+\cfrac{1}{3}}}\qquad \frac{9}{13}=\cfrac{1}{1+\cfrac{1}{2+\cfrac{1}{4}}}\qquad \frac{11}{16}=\cfrac{1}{1+\cfrac{1}{2+\cfrac{1}{5}}}$$

The numerators and the denominators of the proper fractions of these series have constant successive differences.

The last denominators in these continued fractions represent the ratios of the contiguous intervals of the diagram introduced in the second or third turns by the third or fourth leaves. Only the first two fractions in each of these series conform to the above law. The others, like $\frac{4}{7}$ and $\frac{5}{9}$, violate the law early in the cycle; and this explains the absence of them from natural arrangements of the spiral type. The property common to the latter resembles what we have observed in the arrangements of whorls, namely, that the leaves of successive whorls are so placed that those of the upper one fall over the middle positions of the spaces between those of the lower one; but those of the next one above, or in the third whorl, are thus made to fall directly over the leaves of the first. Two whorls thus constitute a cycle, in the sense in

which this name is applied to the spiral arrangements; and in respect to their distributive and cyclic characters, whorls are thus most closely related to the $\frac{1}{2}$, or alternate system. But there is, as I have said, no fundamental or genetic relationship between them and this particular form of the spiral arrangement. The relationship is rather an adaptive or analogical one. They are, so to speak, two distinct solutions of the same problem, two modes of realizing the same utilities, or securing the same advantages; like the wings of birds and bats.

One of these utilities we have now sufficiently considered, namely, that which the theoretical angle k would realize most perfectly; by which the leaves would be distributed most thoroughly and rapidly around the stem, exposed most completely to light and air, and provided with the greatest freedom for symmetrical expansion, together with a compact arrangement in the bud. Neither this property, nor an exact cyclical arrangement, ought, as I have said, to be found, or expected, in the incipient parts at the centre of the bud, any more than the perfected proportions and adaptations of the mature animal could be expected, or are found, in the embryo. Both are fully determined, no doubt, in the vital forces of the individual's growth. Our question is, what has determined such an action in these vital forces? "Their very nature, or an ultimate creative power," is the answer which the theory of types gives to this question. "The necessities of their lives, both outward and inward, or the conditions past and present of their existence," is the answer of the theory of adaptation. Science ought to be entirely neutral between these theories, and ready to receive any confirmation of either of them which can be adduced; though, from this point of view, the theory of adaptation has a decided advantage; since the theory of types can have no confirmation from observation except of a negative sort, the failure of its rival to show conclusive proofs. But we have seen that whatever can be said in favor of the view, that there is a unity of type in the intervals of spiral arrangements, is directly convertible to the advantage of the theory of adaptation; since this unity consists in the distributive property common to these arrangements.* Natural Selection, however,

* There is a remarkable analogy between this relation and that of the two theories of the structure of the honey-cell. The work of the bees suggests to the geometrician a perfectly definite and regular form, which he finds to be the most economical form of compartments into which space can be divided; or he finds that the honeycomb would be the lightest, or be composed of the least material for the same capacity and number of compartments, if partitioned into such figures as the typical cell. From the definition of this figure he is able to compute its angles and proportions with a degree of precision to which the bees' work only roughly approximates at its best, and from which it often deviates widely. The theory of types regards this ideal figure as a determining

or the indirect agency of utility in producing adaptations, cannot, so far as we have yet seen, be appealed to for the explanation of the spiral arrangements in general; nor for the explanation of the verticil arrangements; though the character in the latter, in which they resemble the alternate system, may come within the range of this explanation through the utility I have pointed out. The only ground for the action of Natural Selection which I have yet shown is in the choice there is among possible spiral arrangements with reference to this utility; and it appears that the principle is fully competent to account for the relative frequency of these, and the entire absence of some of them from the actual forms of nature.

We now come to the special study of two other features which have appeared in these arrangements, namely, the spiral character itself and the simplicity of their cycles. The cyclic character is entirely wanting in the ideal arrangement of the interval k; but, as I have said, this interval cannot be proved to exist in nature; for even if it did, it would be indistinguishable even from the simple fraction $\frac{5}{8}$. This very fact, however, makes the interval $\frac{5}{8}$, a sufficiently exact realization of the distributive property, according to the degree of exactness with which actual plants are constructed. But $\frac{5}{8}$ is also a comparatively simple cycle, though there would not be sufficient evidence that its cyclic character is an essential one, or other than incidental to the scale of exactness in the structure of plants, if there did not exist several distinguishable and simpler cycles, namely, $\frac{1}{2}$, $\frac{2}{3}$, and $\frac{3}{5}$. The cyclic character of leaf arrangements is, indeed, a more noticeable feature in plants generally than the distributive one. It is obviously essential, and involves on the theory of adaptation some important utility. Whatever this may be, it is clear that it has to be gained by means directly opposed to those which secure distribution; that is, its utility depends on leaves coming together in direction, or being brought nearer to each other than they would otherwise be; instead of their being dispersed as widely and as thoroughly as possible. This utility is obviously to be sought in the internal relations of leaves to each other, or their connections through the

cause of the structure, or as the pattern which guides the bees' instinct towards an ideally perfect economy. But a plainer order of economy, a simple housewifely one, saving at every turn, together with the conveniences and utilities which govern the work of social nest-building insects in general, would result, if carried out to perfection, in the very same form. Hence the theory of adaptation regards the honey-cells as modifications of similar but rougher structures of the same sort, determined by the further utility of simple saving in working with a costly material; and whatever evidence there is that the bees' instinct is determined toward the ideally perfect type of the honey-cell is directly convertible into proofs that it is so determined by these simple conveniences and utilities.

stem, and not in their outward relations, which require exposure, expansion, and elbow-room. The apparently inconsistent means of these two ends are both realized, however, without interference, in the actual cycles of natural arrangements. Through the simplicity of these cycles leaves, not very remote on the stem, are brought nearer to each other, and into more direct internal connection than they would have but for this simplicity; while in the more prevalent natural forms of the cycle leaves, that are nearest to each other on the stem, are separated as widely as is possible under this condition. That this prevalence is due to selection, through the utility already considered, has been shown to be sufficiently probable. I propose now to connect the prevalence of simplicity in these cycles with another utility. Leaves that are successive, or nearest each other on the stem, may be regarded as rivals, and as rendering each other no service. Those that are more remote may come into relations of dependence, one on the other. Between the leaf and the stem the relations of nutrition are reciprocal. At first, and for the development of the leaf, the stem furnishes nutriment to it. Afterwards the leaf furnishes nutriment for the further lateral expansion of the stem. The development of the stem itself, first in length, while the leaves are expanding, and afterwards in breadth and firmness through the nutrition afforded by the developed leaves, has the effect, and, we may presume, the use or function, of a still more important distribution of the leaves than that we have considered. We have hitherto attended only to the distribution effected by the character of the divergences of leaves around the stem. Their distribution along the stem, or their separation by the internodes of the stem, is a still more direct and effective mode of accomplishing at least one of the uses of the property of distribution, namely, exposure to light and air. The special accomplishment of this important end in the higher plants is secured by two different means; by the firm fibrous structure and the breadth of stems, branches, and trunks in grasses, shrubs, and trees, and by the climbing powers and prehensile apparatus of climbing plants; and in the latter we find the highest degree of specialization or development in the vegetable world. The distribution effected by the separation of leaves along the stem in great measure supersedes the value of their distribution around it, so far as the ultimate functions of leaves are concerned, and independently of their relations in development or in the bud; and this gives freer play to the means of securing whatever advantage there may be in the simpler cyclic arrangements, like the $\frac{1}{2}$ and $\frac{2}{3}$ systems. Accordingly we find, in general, the simpler cycles on the stems of those plants that have the

longest internodes; and, on the other hand, the more complicated cycles are found only in cases of very short internodes, or in great condensations of leaves. There is no evidence, however, that in the condensed form in which undeveloped leaves exist in the bud the cycles are any more complicated than on the stem. Nor ought we to expect such evidence; for it is a false analogy that would lead us to seek for types in the early and rude forms of embryonic life; though, if the simpler cycles were really derived from the more complicated ones, rather than from the utility common to all, we ought, by the analogy of embryology, to find some traces of the process in the bud. No doubt the types exhibited by the mature forms of life exist in the embryo or bud, though not in a visibly embodied form; but rather in a predetermined mode of action in vital forces, embodied in gemmules rather than the visible germ. But while the distribution effected by the internodes of the stem thus allows the simpler cycles to occur, it does not account for their occurrence. This, moreover, must depend on relations in mature, or else in growing leaves, to those below them; and not on their earlier relations in the bud; since, as we have seen, the more complicated cycles are the best fitted for these relations, and in mature stems are only found in great condensations of leaves; such as the bud also presents; yet without any greater complication than the stem has. The simplicity of the cycles in stems with long internodes has the effect that the absolute distance between two leaves standing one over the other is not so great as it otherwise would be. There is, no doubt, a disadvantage in long internodes, or in the separation of growing parts by long intervals from their sources of nutrition; a disadvantage, which only a better exposure to light and air for their subsequent functions could compensate. On the theory of adaptation there would seem to be, then, some advantage to the younger leaf in standing directly over an older one, and not far above it; a greater advantage than in any other position at the same height; and this advantage could apparently be no other than an internal nutritive one, having reference to the sources or movements of sap and the nutrition conveyed by it. But sap circulates with nearly equal facility around and along the stem; and if the lower leaf were really a special source of nutrition to the growing one above it, it could furnish nutrition almost as readily to any other position on the stem at the same height as to the point directly above it, or on the same side. The new leaf is not sensibly nearer the market on account of this feature in the arrangement. But may there not be some advantage to the older leaf in standing directly under the

younger? Next to the advantage of being near a market, or a source of supplies, is the advantage of being in the line of traffic. This, indeed, is in part what it is to be a market, rather than a mine. A leaf is not only a productive or industrial centre, but a commercial one. It effects exchanges, both giving and receiving supplies. When mature, or fully established in this capacity, it draws from the roots its raw material of water and mineral salts, and from the air its more costly material, and in exchange sends forth into the great commerce of the stem its wonderfully intricate fabrics of atoms, woven on the sunbeam, its soluble colloids. Now, although sap may flow with nearly equal facility in all directions in the stem, it probably does flow with greatest rapidity in the direct lines of the forces that impel it, the lines of osmotic force. Sap flows most freely from that side of a perforated tree in the Spring which is immediately below the largest branch. This shows that even in the least active condition of the circulation, when the trunk is surcharged with sap, the forces of circulation are not simply diffusive or hydrostatic; and they must be much less so when definite outlets of this supply become established in the growing buds and leaves of the springtime. The character of the circulation is principally determined by the hydraulic action of osmotic forces. Water *may* flow with equal facility in any part of a river-bed, and across as well as along; but it actually does flow fastest along the middle. The growing leaf has different needs from those of the mature one; hence they are not rivals, or competitors in the market, but buyer and seller, or borrower and lender. The mature leaf needs from the stem water and mineral salts; the growing leaf needs the organic materials of new tissues. The mature leaf helps to prepare the latter by concentrating it, withdrawing the water, and adding its own contribution of organic material in return. But while aiding its younger fellow in this way, it is aided in return, or its efficiency is increased, by the increased circulation produced through the forces of movement above it. In place of a glut in the market we have an active exchange. There is, undoubtedly, a tendency in these physiological causes, however feeble, to that vertical allignment of not very distant leaves, which the cyclic character of the spiral arrangements exhibits, and most markedly in the $\frac{1}{2}$ or alternate system.

We have thus assigned more or less probable utilities to two prominent features in the particular forms of the spiral and verticil arrangements of leaves; their distributive and cyclic characters. We now come to a much more obscure problem, which connects the verticil and spiral arrangements in general

with their probable utilities, and through these with their origin in lower forms of vegetable life. But before entering upon the study of this as an actual physical problem, it is necessary to consider what are the real meanings of the terms "spiral" and "whorl." Are they only conventional modes of representing the phenomena of arrangement, or are they strictly descriptive of the facts in their physical connections? About the whorl there can be no doubt. The actual physical connections and separations of leaves in this type of arrangement are directly indicated by the term; but the ideal geometrical line connecting successive leaves in the so-called spiral arrangements may be a purely formal element in the description of them, and of no material account, — a mode of reducing them to order in our conceptions of them, but implying no physical relationships. There are several ways in which we can so represent the features of these arrangements. Connecting by an ideal line (which may have no physical significance) the leaves nearest to each other on the developed stem, and by the shorter way round, is one way, — the more common way of representing their arrangements. The direction in which this should be drawn, whether to the right or the left, is quite arbitrary in the $\frac{1}{2}$ or alternate system. Connecting, for other cases, the leaves in the same succession, but by the longer way round (as I have chosen to do for convenience), is another way. These are distinctly different spiral paths, but not the only ones by which the parts of these arrangements might be represented geometrically. By connecting them alternately, as 1 with 3, and this with 5, &c., and 2 with 4, and this with 6, &c., we would connect the leaves of the various arrangements by two spiral paths, and these either by the longer or the shorter way round. Or again, by connecting the series 1, 4, 7, &c., and 2, 5, 8, &c., and 3, 6, 9, &c., we would include all the leaves in three spiral paths; and so on. In some cases these lines would not be spiral, but the vertical allignments we have considered. For example, in the last case they would be vertical for the cycle $\frac{2}{3}$; since in this the leaves 1 and 4, or 2 and 5, are the beginnings of distinct successive cycles. If the leaves 1, 2, 3, were in this case of the same age, or at the same height on the stem, and were succeeded at an interval on the stem by 4, 5, 6; also coeval, and so on; we would have the main feature of the verticil arrangement, but not the kind of alternation that belongs to natural whorls. Between 1, 2, and 3 in the natural whorl equal intervals exist, namely, $\frac{1}{3}$; and also between 4, 5, and 6, and so on; but between 3 and 4 the interval in natural three-leaved whorls is either

$\frac{1}{6}$, $\frac{1}{2}$, or $\frac{5}{6}$, according as we choose our spiral paths, or determine which member of the upper whorl shall be counted as the fourth leaf. We see, therefore, that there is no continuity or principle of connection between spiral arrangements and the whorls; and, moreover, that these spiral paths are purely ideal or geometrical lines, so far as we have yet seen. Is there any good reason for supposing that the *simplest* of these, which connects successive leaves on the stem the shorter way round, is any less formal or conventional than the others; or indicates a real connection of the leaves on this path, or any closer original real connection among them? There are two significant facts bearing on this question to which I have already adverted. The first is that the natural fractions of the lower group of our table, or those peculiar to the last two series of the theory of Phyllotaxy, represent the less frequent forms of spiral arrangements, and that if the successive members of these arrangements are connected in the usual mode by this simplest path, or the shorter way round, these members are seen to have less angles of divergence than those of the more common arrangements; or are much nearer each other on this line than the others are. We should thus have the fractions $\frac{2}{7}$, $\frac{3}{11}$, $\frac{1}{4}$, $\frac{2}{9}$, $\frac{1}{5}$; all of which indicate comparatively small divergences, smaller than any among the more common ones. The second fact is the observation that these arrangements are relatively more common among fossil plants than among surviving ones. These facts agree well with the supposition that this simplest spiral path is unlike the others, and is not a merely formal assumption for the representation of leaf-arrangements, but the trace of a former physical connection of the members, or even of a continuity of leafy expansion along this path; a leaf-like expansion resembling a spiral stairway. The leaves, according to this supposition, are the relics of segments made in such a spiral leaf-like expansion around the stem; remnants of it grown smaller and smaller, or more widely separated as they became more advantageously situated through the developments of the stem in length and firmness; and expanding, perhaps, in an opposite direction along the leaf-stems; or, losing their leaf-character and expansion altogether, as they became adapted to other uses in the economy of the higher vegetable life, namely, the use of the leaf-stem itself, as in the tendril, and the uses of leaf-like extensions, as in the reproductive organs of the flower. But are there any surviving instances of such continuous spiral leaf-like expansions on vegetable stems; or, in default of these, could there be any utility in such an arrangement itself to justify the supposition of it as

the basis of the development of more special forms? Before considering this question, however, I will consider what other resources of explanation hypothesis can command. The spiral arrangement might be supposed to be the result of a physiological necessity among the laws of growth, through which single leaves would be produced at regular intervals or steps of development, and placed so as to compass the utilities we have already considered, namely, those of horizontal and longitudinal distribution in successive leaves, and vertical allignment in remoter ones. This would account for the spiral arrangements, and it may be a superior mode of growth, or involve some physiological utility; but that it is not a necessity, is proved by the arrangements of the whorl, in which all the members of a group of leaves are simultaneously produced. The existence of the whorl, then, sets this hypothesis aside. Again, we might suppose on the theory of types that these two great types of arrangement are two fundamental facts in the higher vegetable life, parts of a supernatural plan; two aboriginal and absolute features in this plan. But this, as we have seen, is not to solve the problem, but to surrender it; or rather to demand its surrender, and forbid its solution. Again, the production of adventitious buds in plants, or in separated parts of plants, as in cuttings, dependent only, apparently, on a favorable situation for nutrition, is of common occurrence even in the higher plants. If we could suppose that the definite horizontal distributions of successive leaves were wholly superseded in their utility by the distributions along the stem, or that the leaves could thus be sufficiently exposed to light and air; the power of the adventitious production of buds or leaves in favorable situations might have caused an arrangement without this feature of spiral regularity. But they would still be brought into vertical allignments, if the physiological advantage of the simpler cycles, which has been pointed out, be a real and effective one; for even the so-called adventitious production of buds may reasonably be supposed to be governed by supplies of nutriment. Moreover, these vertical lines would be placed at equal intervals around the stem, on account of the advantage there would be in such a distribution, both for internal and external nutrition. But though leaves would thus be placed at convenient distances along equidistant vertical lines, there would be no consideration of utility to govern their relations to each other on different lines, so as to throw them into whorls, or into definite spiral arrangements. It might, however, be advantageous for leaves on a line between two others to be placed in intermediate positions with respect to the leaves

of these two, and if the latter were placed at the same heights we should have a sector of three whorls; that is, two leaves of the highest and two of the lowest whorl, and one leaf of the intermediate whorl. But such an arrangement disregards or sacrifices in the structure of the whorl itself the advantage, if it be one, of such an alternation. It cannot be reasonable to suppose that a leaf on an intermediate line would seek distance and isolation from those of the lines beside it, and, at the same time, seek close connection horizontally with those of its own whorl. This would be directly opposed to the accommodation of uses in spiral arrangements. The structure of whorls, and the alternation in successive ones, appear, therefore, to be of distinct origins. Whatever advantage there is in the former appears to be sacrificed by this alternation, and by the spiral arrangements; or, if it be a disadvantage, it is avoided by these. It is probably on the whole a disadvantage; since it is ill-fitted for great extensions and branchings in stems, for which the simpler spiral arrangements appear peculiarly fitted. This contrast, however, cannot be regarded as the origin of the contrasted types themselves, and the soundest conclusion appears to be, that, whatever adaptations they may have, these are only incidental, and are not concerned in their origination, either directly through physiological laws of growth, or indirectly by Natural Selection. They are properly genetic characters. This is confirmed by the fact that the particular arrangement for each plant is provided for, or already completed in the bud; that is, it is not a result of laws of development in general, but of the special nature of the plant, or the predisposition of its vital forces. In regard to the causes which I have supposed to control the so-called adventitious production of buds or leaves, it should not be supposed that these exert in actual plants any considerable influence; though the plant's particular laws of growth are probably not in opposition to them. They should only be considered as modifying agencies reacting on the formative forces; but they fail, as we have seen, to account for the spiral and verticil arrangements, and their contrasts through any utility which could modify these forces. But in concluding therefore that these general types of arrangement ought to be regarded as only genetic characters in the higher plants, and as presenting no important advantage or disadvantage, independently of the special forms which they have acquired, or in present forms of life; we are not precluded by such a conclusion from the further inquiry as to what *former* advantage there could have been in less specialized forms, before these genetic characters had lost their

special significance (if any ever existed), and when they could have stood in more immediate and important relations to the conditions of the plant's existence. In this inquiry our principal guide must be hypothesis, but it will be hypothesis under the check and control of the theory of adaptation. It will not be legitimate to assume any unknown form as a past form of life, and as a basis for these arrangements, without showing that such an hypothetical form would have been a useful modification of a still simpler one, which still exists and is known. In this way we may be able to bridge over the chasm that separates the higher and lower forms of vegetable life.

Our problem then becomes, Whether, in the absence of any surviving instances of continuous spiral leaf-like expansions on vegetable stems, we can find any utility in such an arrangement that could act to modify simpler known forms, and convert them into this? If we suppose our hypothetical spiral leaf-blade to be untwisted, it becomes a single-bladed frond, or a frond with one of its blades undeveloped. In considering what advantage there could be in the twist, we should revert to the general objects or functions of leaf-like expansions. They are obviously to expose a large surface to the action of light on its tissues, and to bring it into the most complete contact with the medium in which the plant lives,—with water, or, in more advanced plants, with the air. Secondly, to accomplish this with the least expenditure of material; not by an absolute, but a relative economy, which has reference to the needs of other parts, like the stem or the roots. In many of the higher plants the developments of the stem serve to diminish to the utmost the amount of this material, and the needed expansion, by giving to them advantageous positions. The first of these objects is secured in the simplest and rudest manner in the *algæ*, as represented by the seaweeds. This is a simple expansion of cellular tissue. But even here we do not find perfectly plane surfaces, facing only two ways, and allowing the water to glide smoothly and unobstructed over them. The corrugated surfaces of many of them, and in the large leaves of some land-plants, are doubtless due to unequal growths in the cellular tissues; but such a physiological explanation of this feature does not preclude the supposition of its being a fixed character in a plant, or becoming such in consequence of its utility. It certainly serves the purpose of opposing the leaf-surface to many directions, both with reference to the incidence of light, and to the movement of the surrounding medium,—to water-currents, or to breezes. *Segmentation*, again, such as is seen in the

fronds of brakes or ferns, is another way of bringing the moving medium to impinge on the leaf-surface; but the feasibility of this depends on the fibrous framework which the leaves of land-plants have acquired for the support of their softer tissues. Such a segmentation also appears among the higher plants in compound leaves and in whorls; and, indeed, the whole foliage of trees and shrubs may, from this point of view, be regarded as the reduced segments of the blades of branching fronds, turned in all directions in search of light, and inviting the movements of air through their expanded interstices. Such is the kind of utility that may be claimed for the structure of our hypothetical spiral frond. Another utility in this structure is obvious when we consider the transition of plant-life from aquatic conditions to those of the dry land and the air; as vegetation slowly crept from its watery cradle, or was left stranded by the retiring sea. In default of strength in its material, such as a slowly acquired fibrous structure or framework ultimately gave to it in this transition, the *strongest form* would be the most advantageous in sustaining the weight of the no longer buoyant plant. A spiral arrangement of the blade around a comparatively firm, and, perhaps, already somewhat fibrous stem, would come nearer fulfilling this condition than any other conceivable modification of the frond.

We have, so far, in conformity to the spiral arrangement in leaves, supposed this twisted frond to be a single-bladed one, or with only one blade developed. This would be a first step in that reduction of leaf-expansion which a more advantageous situation of it would allow; and might be required, even at this early stage of atmospheric plant-life, on account of the greatly increased importance of the roots and stem. But this hypothesis is not necessary in general for the ends we have considered. A two-bladed frond might be similarly twisted and give rise to a double spiral surface like a double spiral stairway, or like the blade of an auger; or such a surface as the two handles of the auger describe as they are revolved, and, at the same time, carried forwards in the direction of the boring. The simplest segmentation of such a twisted frond, after the stem had acquired sufficient strength, and such a subsequent reduction of the segments as might be required for the nutrition of the stem, would give rise to parts, which, turned upwards to face the sky, and also separated, perhaps, by the growth of internodes in the lengthening stem, would result in what we may regard as the original form of whorls, namely, a continuous leaf-like expansion around the stem. The origin of the whorl arrangement itself would thus

be distinct, as we have found that it ought to be, from the origin of the relations in the parts of whorls to one another, and to those of adjacent whorls. These would be results of a subsequent segmentation, and would be determined by the utilities which we have considered in this and in the spiral arrangements. And so both this and the spiral arrangements as general types of structure, though originating, as I have supposed, in useful relations to former conditions of existence, may be regarded in relation to later developments as useless, and merely inherited or genetic types; the bases on which subsequent utilities had to erect existing adaptations of structure. The segmentation of the single spiral frond would at first have little or no relation to these more refined utilities of arrangement, but out of all the variable and possible arrangements so produced there would be a gradual selection, and a tendency toward the prevalence of those special forms, which are at present the most common ones. The typical or unique angle of the theory of Phyllotaxy would thus appear to be the goal toward which they tend, rather than the origin of the spiral arrangements. But since a simple cyclic arrangement appears to have also an important value, we cannot concede to the typical angle the exclusive dignity of even this position.

The segmentation I have supposed in this process should not be regarded as an hypothetical element in it; since it is a well-established law of development. Distinct organs are not separately produced from the beginnings of their growth, but make part of their progress in conjunction, or while incorporated in forms, from which they become afterwards separated; and become then more and more special in their characters, or different from other parts. It is this differentiation and separation of parts out of already grown wholes which distinguishes development from mere growth. The analogy of the phases of development in embryonic or germinal life to development in general is liable, however, to be carried too far; and the fact is liable to be overlooked, that these phases of growth are special acquisitions of the higher forms of life, which have features of adaptation peculiar to them. But the more general features of them, and the useless, or merely genetic phases, may safely be regarded as traces of past characters of adaptation, which a change in the mode and order of individual development has not obliterated; while new adaptations have been added, that have no relation to any past or simpler forms of life, but only to the advantages which embryonic or germinal modes of reproduction have secured. If we should follow out the phases of general

development in the progress of the leaf along the line of its highest ascent in development, from the segmentations we have supposed in the twisted frond, we would soon arrive at the steps already familiar in the principles of vegetable morphology. In these we have the same law of segmentation or separation of parts, and the same successive relations of genetic and adaptive characters. What was produced for one purpose becomes serviceable to a new one; and in its capacity as a merely genetic character, or as an inherited feature, becomes the basis for the acquisition of new adaptations. Thus the fibrous structure, at first useful in sustaining the softer tissues of the leaf, becomes the means of a longitudinal development of it, and its more complete exposure to light and air by the growth of the foot-stalk. This stalk acquires next a new utility in climbing-plants to which it becomes exclusively adapted in the tendril. The adaptive characters of the tendril are its later acquisitions. Its genetic characters, such as its position on the stem, and its relations to the leaves, become useless or merely inherited characters. The contrast of genetic and adaptive characters appears thus to have no absolute value in the structure and lives of organisms, but only a relative one. The first are related principally to past and generally unknown adaptations; the second to present and more obvious ones.

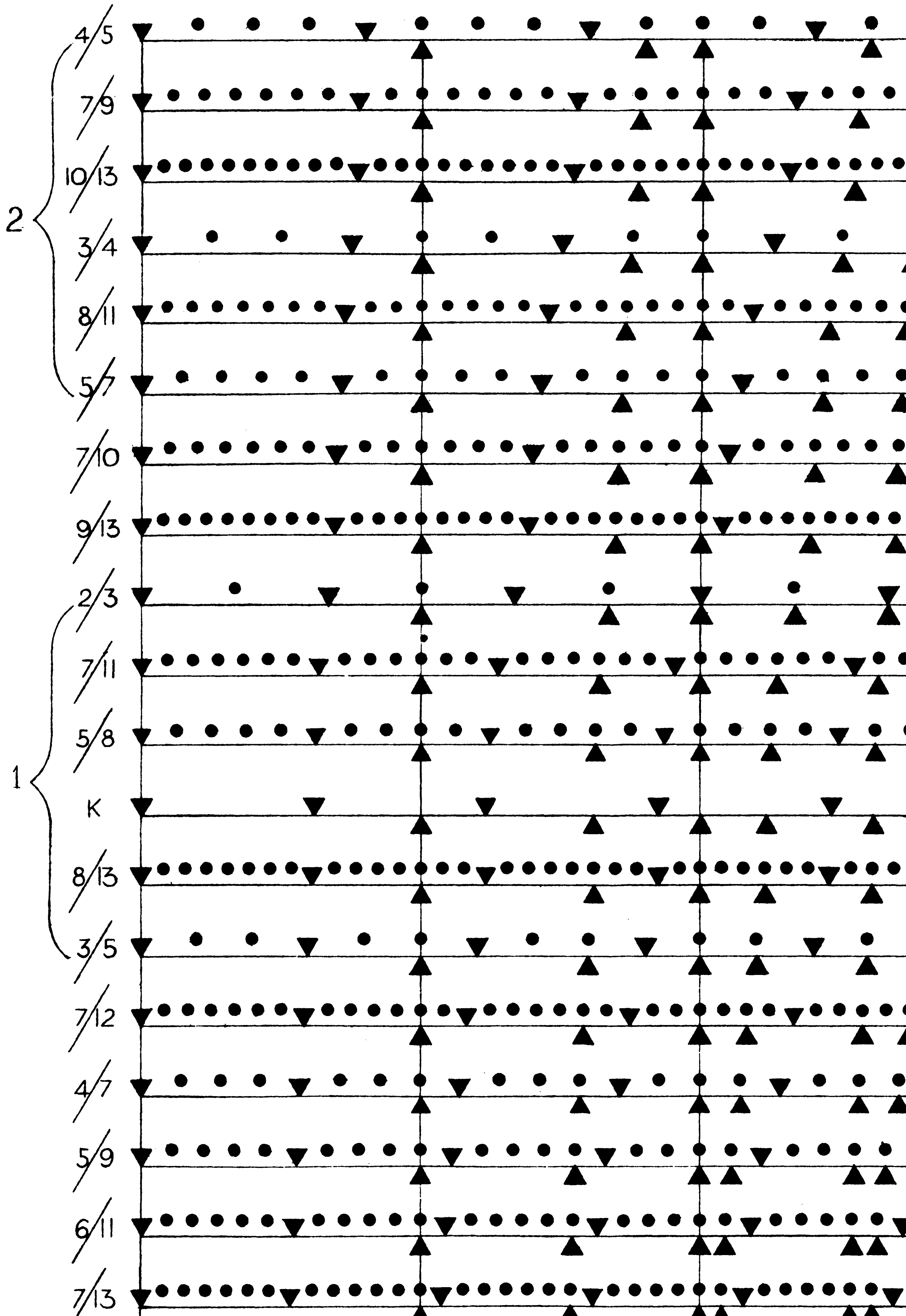
In accordance with this law I have supposed that the general features of the two types of leaf-arrangement, for which no present utilities appear in the lives of the higher plants, were nevertheless useful features in former conditions of vegetable life. The more special features of these arrangements should not, from this point of view, be regarded as derived one from another, much less from the typical or unique form of the theory of Phyllotaxy. In one sense they may, indeed, be said to be derived from this form, at least some of them; yet not from it as an actually past form or progenitor, but rather from the utility which it represents in the abstract. I have, however, pointed out that another utility, shown in the simpler cyclic arrangements, has an equal claim to this spiritual paternity. The actual forms of the spiral arrangements in leaves should, therefore, be regarded as forms independently selected, and as selected on the two principles of utility, which we have considered, out of a very large variety of original forms. We have seen that even those forms which survive include almost all possible ones that could be distinguished; though the more prevalent ones are at present in the minority. We have also seen that the latter fact, and the more frequent occurrence of inferior

forms among fossil plants, are almost the only grounds on which the inductive foundation of the theory of Phyllotaxy could be regarded as well established. On these grounds, and on this foundation, I have sought by hypothesis to reconstruct the continuity of higher and lower forms in vegetable life; and through this to find the *origin* of the principal types of arrangement in leaves. The speculation lies wholly within the limits prescribed for legitimate hypothesis in science. It does not assume utilities in themselves unknown, but assumes only unobserved or unknown applications of them, and raises to the rank of essential properties relations of use, which, at first sight, appear to be only accidental ones. Attention may be claimed at the least for it as an illustration of the method by which the principle of Natural Selection is to be applied as a working hypothesis in the investigations of general physiology or physical biology.

Many features in the structure of leaves, not relating to their arrangements, fall beyond the proper province of this inquiry, but equally illustrate the relative nature of the distinction between genetic and adaptive characters. The general character common to all leaves and leaf-like organs has an obvious utility with reference to the function of nutrition. Some special modifications have the purposes of defence, as in the thorn; of mechanical support, as in the tendril; and of reproduction, as in the parts of the flower. But the vast variety of forms which leaves and the parts of flowers present do not suggest any obvious uses. On the theory of adaptation they would naturally be referred to a combination of adaptive and inherited features. A fixed proportion between the two principal tissues in a plant due to some past utility may, without being changed, become adapted to new external relations, or to new physiological conditions, through various arrangements of them in the structure of the leaf; and this would give rise to a great variety of forms. The forms of notched and sinuated leaves are referable to that process of segmentation and reduction in leaf-expansions, which we have seen to be so important a process in the derivation of the higher plants. But another principle of utility comes into play in the lives of the higher plants, similar to that which appears to be the origin of some of the more conspicuous external characters of animals, namely, what produces distinguishableness and individuation in an animal race. No doubt the laws of inheritance and Natural Selection account for much of the character of individuality in races, or for the fact that variation has a very limited range compared to the differences between species, so

far as it affects any useful quality or character. But variation, not only in animals, but also in many of the higher plants, is much more limited than these causes seem capable of accounting for. It is, apparently, as limited in respect to useless though conspicuous features as in those that are of recognized value to life. Sexual Selection, through which the characters of animals are chosen by themselves, or brought into relation to their perceptive and other psychical powers, is the cause assigned for this fact in the case of animals; that is, forms are chosen for their appearance, or for the pleasure they give to the senses. But plants have no senses, except a sense of touch; and they have no other known psychical powers. Nevertheless they present many conspicuous features of beauty to the eye, and many give forth agreeable and characteristic odors. And such characters are apparently as fixed in many of the higher plants as in animals. The theory of types and the doctrine of Final Causes regard this fixedness and individuality as ends in themselves, or else as existing for the service of some higher form of life, or ultimately even for the uses of human life. But the theory of the adaptation of every feature in a form of life to its own uses is not without resources for the explanation of these characters in plants; for though the plant has no sense to appreciate, or power to select, its own features of individuality and beauty, yet the lives of many of the higher plants are essentially dependent on such powers in insects; so that whatever character renders them attractive to insects, or distinguishable by their sight, may be said to be of use to plants for the ends of reproduction, and tends in this way to become a fixed or only slightly variable character. That this cause may have acted not only to determine definite shapes, colors, and odors in flowers, but also definite features in the foliage of plants, as the marks or signs of these, and that the value of such signs may have determined a greater degree of fixedness or constancy in the arrangements, as well as in the shapes of leaves, is an hypothesis that may be added to those we have already considered, concerning the utilities of these arrangements. This cause would tend to give prominence to those features in arrangement which are most conspicuous to the eye, namely, those of cyclic regularity and simplicity. Such an explanation of this cyclic character, or the simple and definite arrangements of leaves at short intervals in vertical lines on the stem, or the utility of this as a distinguishing character of the plant, is not inconsistent with the physiological utility in these arrangements, which I have pointed out; but the two in co-operating to the production of the same forms would illustrate a

principle in the economy of life which has a wide application, — the principle of indirect utility or correlative acquisition, dependent on ultimate laws in physical and mental natures, — through which independent utilities are realized by the same means, or the same means made serviceable to more than one distinct end. In such ultimate, underived relations of adaptation in nature, we find principles of connection and a unity of plan which cannot be referred to any accidents of history or development.



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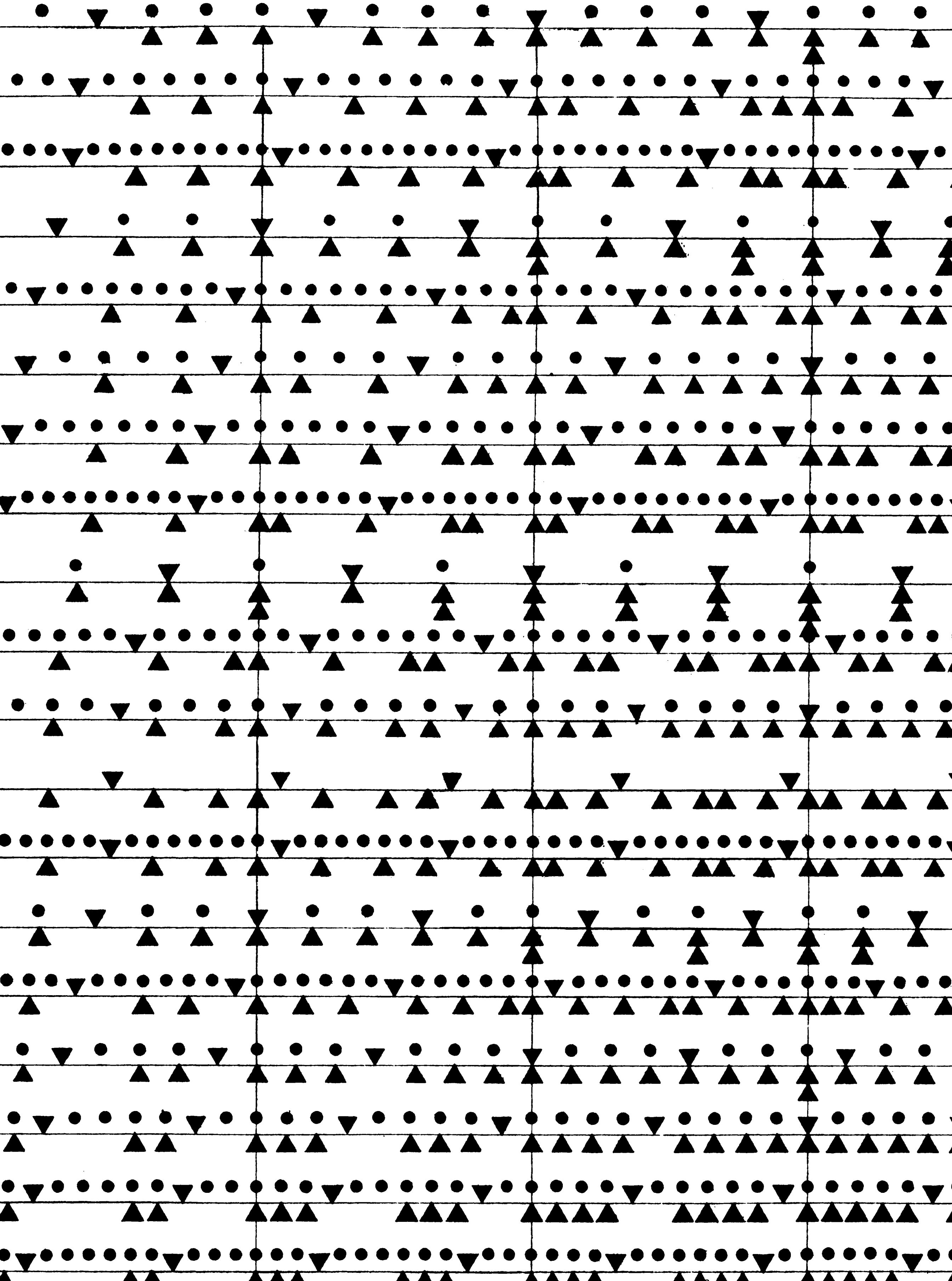

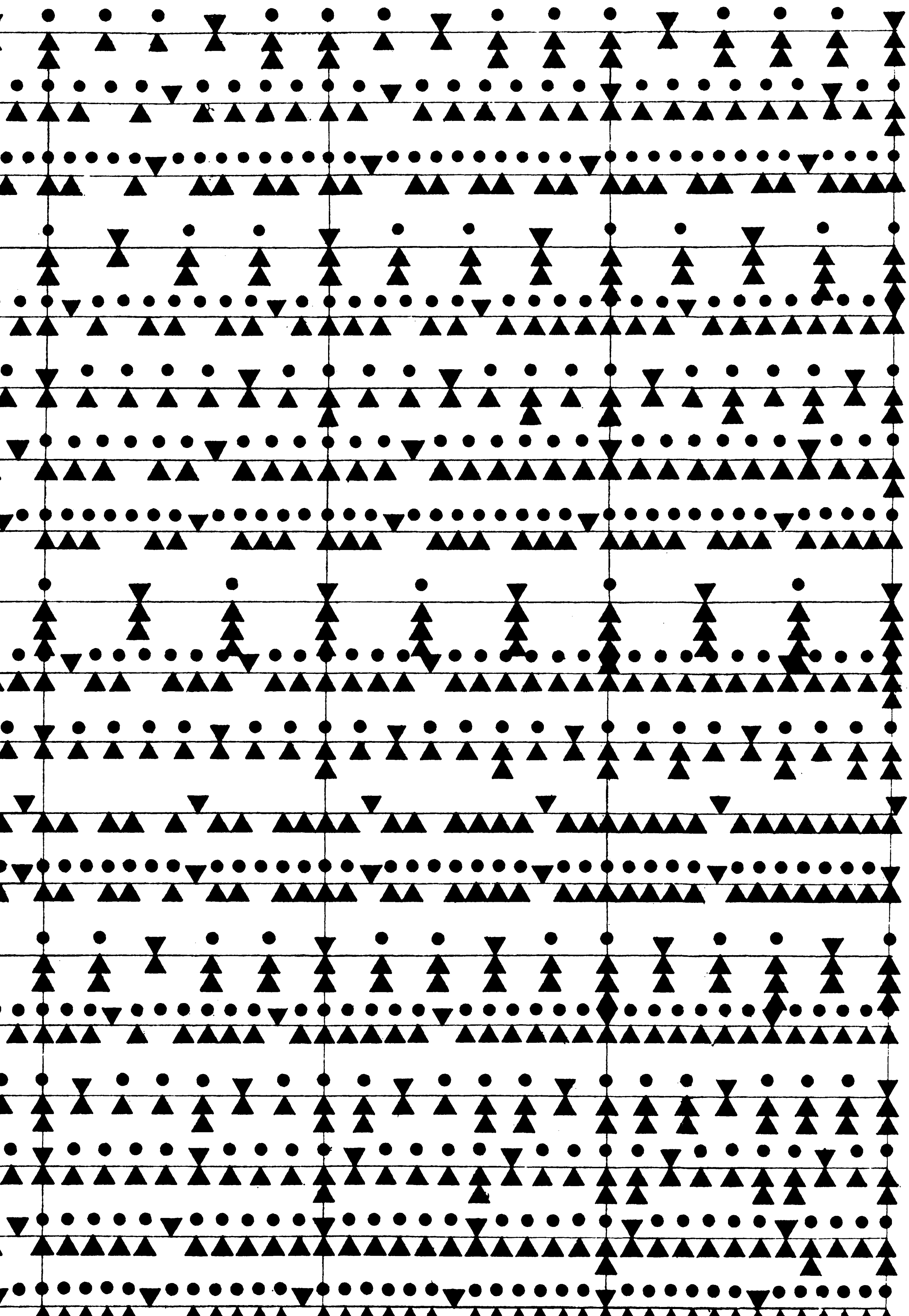

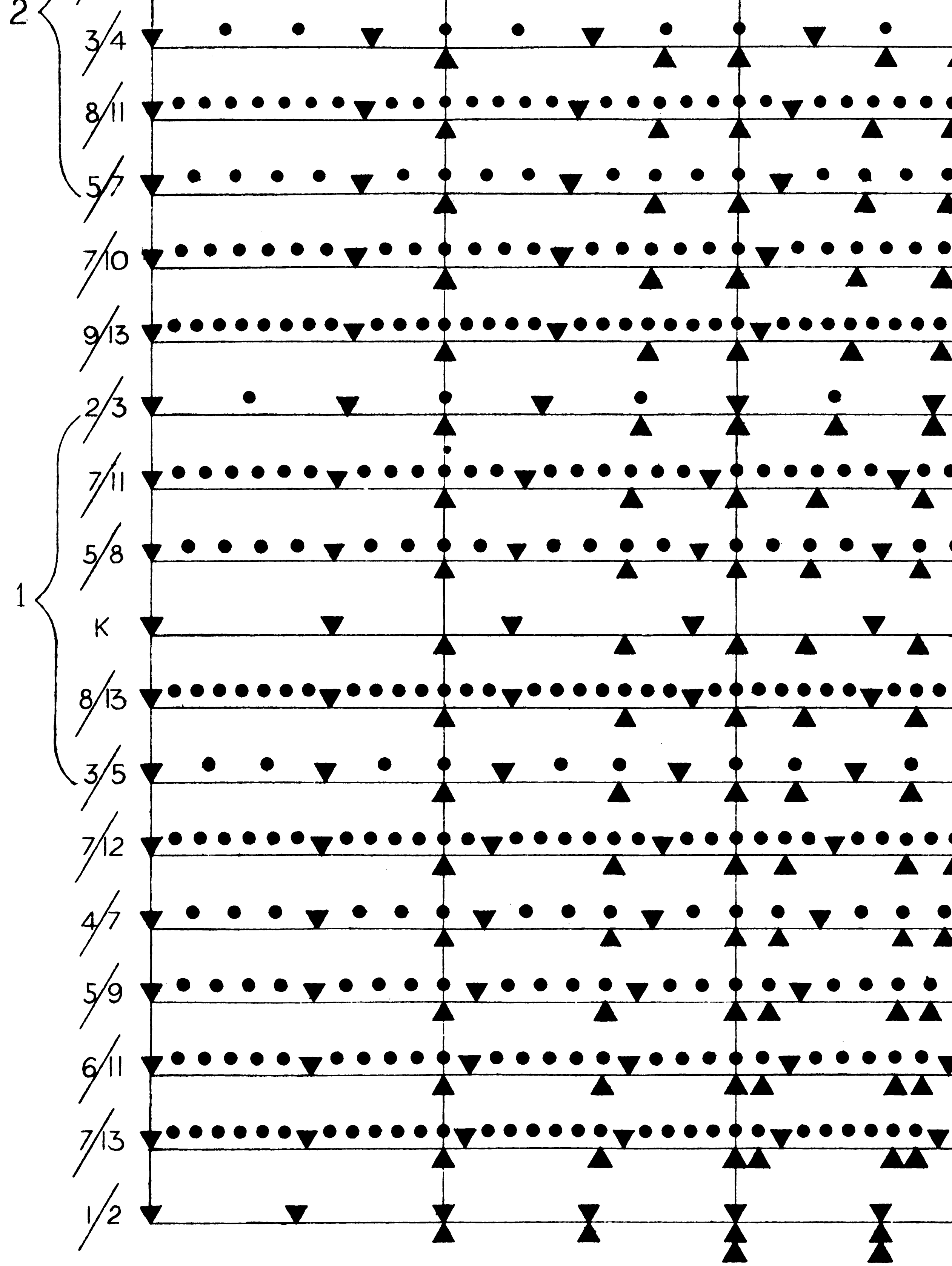

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